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THE CONTROL OF THE CITROPHILUS MEALYBUG, PSEUDOCOCCUS GAHANI, BY AUSTRALIAN PARASITES[1,2]

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INTRODUCTION

The general disappearance of injurious infestations of citrophilus mealybug, *Pseudococcus gahani* Green, in California, is attributed to the work of *Coccophagus gurneyi* Compere and *Tetracnemus pretiosus* Timberlake, two internal parasites introduced into California in 1928 from Sydney, Australia, by the University of California Citrus Experiment Station. Since 1929, after the general establishment of these parasites, the mealybug has been scarcer than at any other time since it became a major pest. This scarcity of mealybugs has been continuous without appreciable annual fluctuations. No damage has been reported in the areas where the parasites have been established for a period of about two years, nor has it been necessary to liberate *Cryptolaemus montrousieri* Mulsant to prevent the citrophilus mealybug from increasing to injurious numbers.

The saving resulting from the work of *Coccophagus* and *Tetracnemus* may be estimated from the saving in Orange County, where more than 40,000 acres of citrus were infested and where surveys show that the parasites have prevented the recurrence of infestations that were estimated to be costing the growers $500,000 to $1,000,000

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annually. This saving is for that county only and is aside from the cost of *Cryptolaemus* production. In Los Angeles County, and other counties along the coast, the saving has been less than in Orange County. The infestations were less extensive and generally less severe in the other counties because of unfavorable climatic factors which tend to retard the development of the citrophilus mealybug.

Prior to the introduction of *Coccophagus* and *Tetracnemus* the mealybug situation was not entirely satisfactory. By 1929 approximately 75,000 acres of citrus were infested by the citrophilus mealybug. Over the greater part of this acreage the infestations were kept in check by *Cryptolaemus;* but, in spite of the good work of *Cryptolaemus,* each year an increasing number of severe infestations developed. The degree of control obtained by the use of insectary-grown *Cryptolaemus* compared favorably with the results obtained by spraying and fumigation against other citrus pests. In addition the biological method had the advantage of being comparatively cheap, the *Cryptolaemus* production for the entire infested acreage costing only $125,000 annually as compared with $35 to $40 per acre for spraying or fumigating of citrus infested with red scale or black scale. A direct comparison of the cost of controlling citrophilus mealybugs on citrus by *Cryptolaemus* with the cost of mechanical control cannot be made, for, regardless of cost, neither fumigation nor spraying has satisfactorily controlled mealybugs on citrus in California.

In 1927 some of the leading orchardists resorted to water-washing as a means of preventing the damage that results from serious mealybug infestations. Some 15 or 20 growers equipped their orchards with expensive systems of water pipes for washing the infested trees, and a concern in Santa Ana was engaged in manufacturing and installing water-washing equipment in citrus orchards. The situation made it imperative that a search be undertaken, having as its objective the discovery of additional natural enemies of the citrophilus mealybug.

THE SEARCH FOR THE NATIVE HOME OF PSEUDOCOCCUS GAHANI

The possibility of obtaining effective internal parasites of the citrophilus mealybug to bring about a more satisfactory natural control had been long recognized by entomologists engaged in biological control work in California. In 1927, when the mealybug situation became alarming, the Citrus Experiment Station of the University of California decided to send a collector abroad in an effort to secure

additional natural enemies of mealybugs. This project was under the direction of Harry S. Smith, and Harold Compere was assigned to make the trip.

The citrophilus mealybug was obviously an introduced pest, but the country of origin was unknown to entomologists. It was known to occur in the British Isles, where it was first described in 1915, but the evidence indicated that it was a recent introduction and not indigenous there. G. F. Ferris (1927) recorded the discovery of the citrophilus mealybug in South Africa. It was taken there under circumstances which led him to state that there was not any likelihood that South Africa was its native home. C. P. Clausen had searched unsuccessfully for the citrophilus mealybug in China, Japan, the Philippine Islands, and Formosa. Silvestri, then employed by the University of California, covered much of the territory explored by Clausen, and in addition Indo-China, without finding this mealybug. S. I. Kuwana, chief entomologist of the Japanese Empire, who is a specialist on the Coccidae of the Orient, had never found the citrophilus mealybug. Southern Europe was excluded as a possible place of origin, because it did not seem probable that the mealybug could have existed there without having been discovered. The occurrence of this pest in widely separated countries was sufficient grounds for the belief that it had been accidentally transported by commerce. It was assumed that the citrophilus mealybug originated in a country having a subtropical climate comparable to the coastal area of southern California and one which was closely linked by steamer transportation with California, South Africa, and the British Isles. On the basis of this reasoning it seemed that Australia was a likely place in which to search for the native home of this species. The climate of Sydney does not differ greatly from that of southern California and it is one of the world's greatest shipping centers, having regular and direct steamer communication with California, South Africa, and the British Isles.

Discovery of Pseudococcus Gahani in Australia.—On September 27, 1927, Compere discovered seven overwintering citrophilus mealybugs wedged between the scales of unopened buds on a *Choisya ternata* growing in the Sydney Botanical Garden. This early discovery was rather remarkable; for it was made shortly after beginning a plant-to-plant inspection of the garden on the first day spent in searching. It was not until several weeks later that additional specimens of the citrophilus mealybug were discovered on other host plants; the species was never again collected on *Choisya*. The collector of parasites of Coccidae usually first examines plants in botanical

gardens, estates, and residential areas where various assortments of plants are grown, for in such places there is usually found a representative assemblage of local and introduced coccids, as well as their parasites.

The discovery of *Pseudococcus gahani* Green in Sydney immediately brought up the question as to whether it was native there or a recent accidental introduction. If native it would presumably be attacked by specific parasites. Parasitism was first found on October 21, 1927, when a mealybug that had been cleared and stained was being studied microscopically. The stained mandibles and head capsule of a parasitic larva were clearly revealed through the transparent integument of the mealybug. The identity of this larva was never determined. It was not one of the species introduced into California. Possibly it was the larva of *Anusoidea comperei* Timberlake.

Control by Parasites—The evidence is now fairly conclusive that in Australia the citrophilus mealybug is held in check through the influence of parasites. When it became apparent that *Pseudococcus gahani* was very scarce in Sydney, the possibility that an adverse climatic factor might be mainly responsible for its scarcity was considered. It was felt that the finding of a heavy infestation fully exposed to the weather would eliminate this possibility. The cottony cushion scale, *Icerya purchasi*, the outstanding example of a pest controlled by natural enemies, offered a clue. In California occasional severe infestations of cottony cushion scale develop on isolated plants located in places not readily reached by natural enemies. These sporadic, isolated infestations usually develop in places out of the usual range of insects, such as on dooryard or porch plants, or on plants in hotel lobbies in the business or industrial sections of large cities.

This knowledge of *Icerya* prompted a search in the center of Sydney's industrial district, seemingly the most unlikely place to repay the visit of an insect collector. On the first day's search, an acacia tree was found which was heavily infested with cottony cushion scale. This seemed to justify the belief that possibly a severe infestation of *Pseudococcus gahani* could be found in the same area. On the second day's search, January 13, 1928, an old mulberry tree in the yard of a small dwelling at 192 Bulwara Road, Pyrmont, was found to be heavily infested with citrophilus mealybug. The tree was fully exposed to wind and rain. Cottony secretions hung in festoons from the under sides of the limbs, and the ground beneath the tree was sprinkled with gravid mealybugs which had either migrated

or fallen from the tree. A photograph of this tree, taken after three of the largest limbs had been removed and packed for shipment to California, is shown in figure 1. When the tree was found, no evidence of parasitism was noticed, and the mistake was made of supposing it to be an infestation free of parasites because of its isolation and inaccessibility.

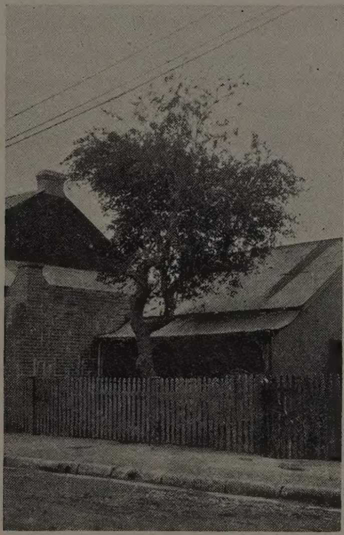

Fig. 1. Mulberry tree, Bulwara Road, Sydney, that was heavily infested with *Pseudococcus gahani* Green. (The photograph was taken after infested limbs were removed.)

An Attempt to Secure Parasites by the Use of Traps.—Prior to the discovery of the heavy infestation of *Pseudococcus gahani* in January, comparatively few specimens of mealybugs were collected. When it became apparent that only occasional parasitized *P. gahani* could be found under natural conditions, an attempt was made to attract parasites to mealybugs on plants which had been purposely infested in the laboratory and then placed in the open in proximity to plants growing in places where the parasites were known to occur. Twelve small oleanders in pots were stocked with mealybugs. When the plants were thoroughly infested they were placed in various districts under shrubs and trees where mealybugs had previously been collected. One week later, when the first inspection was made, it was found that all the mealybugs had disappeared from the trap plants.

The disappearance was attributed to heavy rains accompanied by high winds, which were thought to have dislodged the mealybugs and washed them away.

Propagating the Parasites.—Plans were made to operate a small insectary when the first specimens of *Pseudococcus gahani* were discovered on September 27, 1927. Sprouted potatoes, trays, cages, and the usual paraphernalia necessary for propagating mealybugs were obtained. Of the seven mealybugs discovered on the *Choisya ternata*, three of the smallest were left undisturbed so that they could reproduce on the plant; the two largest specimens were prepared for microscopic study, to verify the field determination; and two specimens were placed on a potato sprout and confined in a jar so that they could reproduce.

As the season advanced and the weather became warmer, scattered specimens of *Pseudococcus gahani* were collected on certain grevilleas and oleanders in the Botanical Garden. These specimens were usually found associated with the long-tailed mealybug, *P. longispinus* (Targ.). *P. gahani* was rare; on some days no specimens were found, and at other times four or five specimens were obtained as the result of a day's collecting. Searching for a period of several weeks in the citrus orchards within a 25-mile radius of Sydney resulted in the collection of a total of only 69 specimens on citrus, practically all of which were taken singly.

Except for occasional specimens that were prepared for microscopic study, all healthy-looking mealybugs were placed on potato sprouts in cages in the laboratory. If the mealybugs showed signs of parasitism they were isolated in vials. There was no way of detecting and segregating the mealybugs which contained eggs or young larvae of parasites. Because of this, some parasitized mealybugs were introduced into the breeding stock. Adult parasites eventually issued from the parasitized mealybugs placed in the cages. All parasites were captured and transferred to separate jars or cages as soon as they were seen. At the time it was thought that this procedure would maintain a balance between the numbers of parasites and their hosts and that the stock of both parasites and mealybugs could be kept indefinitely. However, the efficiency of the parasites and the rapidity with which they could breed were not fully appreciated. Some of the parasites oviposited in the mealybugs reserved for propagation before they were captured and removed to separate cages.

About the first week in January, 1928, it became apparent that too many parasites had been permitted to develop and that all the cages reserved for propagating mealybugs were infested with them. The

situation was further complicated by excessive rotting of the potatoes which were depended upon for propagation of the mealybugs. A continuous supply of mealybugs could not be maintained to carry the parasites generation after generation without a continuous supply of potato sprouts. Ten sacks of certified, supposedly disease-free potatoes had been placed in cold storage to be used when mature potatoes were no longer available and before potatoes of the new crop would sprout. When the cold-storage warehouse was visited for the purpose of getting a sack of potatoes, it was found that the potatoes were almost a total loss as a result of rots of the most virulent types. Enough sprouts were available in January to continue the work for a month or six weeks. Because of horticultural quarantine restrictions, green lemons or other fruits could not be used to propagate mealybugs destined for shipment to California. The finding of a large quantity of mealybugs on the mulberry tree, January 13, 1928, temporarily provided plenty of hosts for the parasites that had accumulated, but not enough potato sprouts were available to care for the mealybugs from this source.

Transporting the Parasites.—Because of the presence of diseased potatoes scattered through all the cages, the material was considered unfit for a long-distance shipment in tightly closed boxes. Several possible ways of shipping the parasitized mealybugs to California were considered, but the best plan seemed to be that of personally transporting the entire lot of material on the first steamer leaving for the United States. The decision in favor of this plan was influenced by the fact that an immediate departure would make it possible to transport the entire stock safely at one time. The other alternative was to make small shipments while at the same time endeavoring to preserve a breeding stock at Sydney throughout the winter months without sufficient host material. The latter plan would have necessitated the destruction of a major portion of the natural enemies to preserve a balance between parasites, mealybugs, and potato sprouts; while the former plan offered the inducement that if the parasites should prove successful in California their establishment in large colonies at an early date would be a decided gain. Approval of the plan to return to California was secured by cable, and arrangements were made to depart on the steamship Tahiti, February 23, 1928.

On February 20, the infested tree at Bulwara Road was visited with the supposition that no parasites occurred there, and with the expectation of obtaining a quantity of unparasitized mealybugs to be used as hosts for the parasites while in transit to California. On the previous visits no parasitism was observed in the mealybugs collected

from the ground or from the low-growing shrubs under the mulberry tree. However, the final inspection revealed a condition quite different from that anticipated, because what appeared when viewed from the ground to be trailing festoons of male pupae and egg masses proved to be the mummified bodies of countless thousands of parasitized immature female and male mealybugs. A more opportune time could not have been selected for the collection and shipment of this material, for the great majority of the parasites were in the pupal stage and about ready to emerge. There were not, however, enough unparasitized mealybugs to provide for the parasites that had been propagated in the laboratory. Because of more or less continuous rains during the week, the material taken from the mulberry tree was sodden with water, and consequently before packing it was spread out to dry in a warm room. The heat of the drying process caused thousands of *Tetracnemus pretiosus* to issue. This material was packed in insect-tight boxes and brought to California in the vegetable room of the steamship Tahiti at a temperature ranging around 38° F. After being unpacked in the quarantine room at Riverside, many thousands of *Tetracnemus* were obtained from the mulberry-tree material.

The horticultural quarantine laws of Australia prohibit the entry of American potatoes into New South Wales and the laws of California prohibit the entry of Australian potatoes. Since the plan was to transport the entire stock of laboratory-grown parasites and their hosts in the ordinary type of ventilated propagating cages, the problem arose of securing host plants not prohibited entry into the United States. All parasites at work in the cages were definitely known to be primaries, and as their host, *Pseudococcus gahani*, was already a pest in California, the entry of these would be permitted. The Australian potatoes on which the mealybugs were growing were prohibited, as were lemons and other hosts of Australian origin.

In order to comply with the quarantine regulations, American-grown potatoes were secured. The steamers of the Matson Line carry American potatoes in their stores of food on the voyage between San Francisco and Sydney. Since the seasons in the northern and southern hemispheres are opposite, potatoes grown in the northern hemisphere sprout readily during December, January, and February, when the southern-grown potatoes are too immature to sprout. The necessity of securing potatoes of American origin was explained to Mr. Butler, Chief Horticultural Quarantine Officer, New South Wales. He very generously cooperated, as did the officials of the Matson Navigation Company, so that two sacks of American-grown potatoes were ob-

tained from the American steamer Sierra. These were permitted entry into Sydney under certain quarantine restrictions, which specified that they were for scientific use, must be kept in cages in the laboratory, and eventually destroyed or shipped out of the country.

The potatoes obtained from the steamship Sierra were selected for their freedom from disease and for the size of their sprouts. Many of them had already produced sprouts 3 to 4 inches long. In preparation for the voyage to California it was necessary to transfer the mealybugs from the sprouts of Australian-grown potatoes to those of American origin.

The identity of the mealybug that was injurious to deciduous fruit trees in New Zealand under the name of *Pseudococcus comstocki* (Kuw.) was questioned. The doubt concerning the identity of the mealybug pest in New Zealand arose because prior to our determination of the Australian specimens as *Pseudococcus gahani* they had been confused with *P. comstocki* (Kuw.). The microscopic characters then used by taxonomists to separate *P. gahani* and *P. comstocki* are not reliable, although in life the two species are reputed to be very unlike and easily separated by the differences of the waxy filaments.

If, as anticipated, the pest in New Zealand should prove to be *P. gahani*, and not *P. comstocki* as recorded, then by going via New Zealand on the steamship Tahiti there would be a chance to obtain an additional supply of mealybugs to supplement the Australian stock on hand. This possibility was explained by letter to D. Miller, Government Entomologist, New Zealand. He was on the dock when the Tahiti arrived at Wellington, February 27, 1928. Because of heavy rains it was impossible to visit deciduous orchards, so several greenhouses were visited where grapes were being grown. In one of these a very heavy infestation of *P. gahani* was discovered and in an adjoining apple orchard a severe infestation occurred. A box of grapes infested with these mealybugs was obtained.

During the three weeks en route to San Francisco on the steamship Tahiti, the procedure was practically the same as that followed while in Sydney. A vacant hospital room, with light and ventilation, was used as an insectary, and the material was tended daily. The potatoes remained in good condition and mealybugs were available in abundance after the material was obtained at Wellington.

At San Francisco it was necessary to remove and destroy all the grapes before the material was shipped to Riverside, because of the quarantine against hosts of the Mediterranean fruit fly.

DESCRIPTION AND BIOLOGY OF COCCOPHAGUS GURNEYI

The first specimen of *Coccophagus gurneyi* Compere was captured alive on an oleander leaf in the Sydney Botanical Garden, and at the time was considered merely a specimen of scientific interest (Compere, 1928). As a general rule, the parasite collector is not interested in specimens collected indiscriminately but is primarily concerned with reared specimens having definite host records. However, because of the collector's particular interest in all species of *Coccophagus* and their host relations, this specimen was kept alive, without any expectation that it would eventually prove to be one of the most valuable parasites transported from one country to another.

Curiosity prompted a few experiments to discover the host of the female *Coccophagus.* The oleander bush on which the parasite was captured was infested with *Aphis nerii* Fons., *Saissetia oleae* (Bern.), *Pseudococcus longispinus* (Targ.), and an undetermined lecanine scale, possibly *S. persimile* (Newst.). It was supposed that one of the lecanine scales on the oleander was the host of this parasite, for prior to the discovery of this species there were only two records (both questionable) of a *Coccophagus* having been reared from anything but lecanine scales. Samples of the two scales were placed in the vial with the *Coccophagus,* but she was not interested in them. The next test was made with oleander aphis, with similar negative results. In the final test two specimens of long-tailed mealybug, *P. longispinus,* were placed in the vial with the parasite. Immediately upon sensing a mealybug, the *Coccophagus* inserted her ovipositor. Since the long-tailed mealybug is not of economic importance in California and the *Coccophagus* was thought to be nothing more than a novelty because of its unusual host, no further special care was given her and she died the next day. The mealybug in which she inserted her ovipositor was subsequently mislaid and lost. At the time it was not known that occasional specimens of *P. gahani* were generally scattered on oleanders throughout the Botanical Garden and the testing of the parasite on them was not considered; for at that time only five specimens of *P. gahani* were available and these were being carefully preserved so that they would propagate.

The second specimen of *Coccophagus gurneyi* obtained was a female. She was dead when discovered and had issued from a long-tailed mealybug that had been isolated in a small vial.

The third specimen of *Coccophagus gurneyi* was also a female. She was reared on November 24, 1927, from a long-tailed mealybug collected under a piece of loose bark in the citrus orchard of Fred Chilton, at Warrawee, about 10 miles from Sydney. This specimen was given special care, since it was then known definitely that *Coccophagus* not only oviposited in mealybugs but also developed in them, and at this date enough citrophilus mealybugs had been propagated so that a few specimens could be spared for experimentation. This *Coccophagus* was confined in a vial with a half-grown specimen of *Pseudococcus gahani*. She immediately oviposited. The next day the mealybug was dissected and eggs of characteristic coccophagine shape and size were observed. On three subsequent days different lots of citrophilus mealybugs were exposed to attack by the *Coccophagus* and after being oviposited in they were transferred to a potato sprout where they were allowed to develop. On November 28, the *Coccophagus* was liberated in a jar with a good supply of citrophilus mealybugs. On following days dissections were made of the mealybugs exposed to parasitism. These dissections showed that the *Coccophagus* eggs had hatched and that the young larvae were growing. It was definitely known that the female *Coccophagus* was a virgin and that probably her progeny would be males, so a sharp lookout was kept for the appearance of a male in order to fertilize her and thus insure female offspring. On December 18, 1927, a male was captured in a cage which was supposed to contain citrophilus mealybugs free from parasites. The original female, reared on November 24, was still alive. She was confined for a few minutes in a vial with the male. Mating promptly occurred and the fertilized female was returned to a special jar and provided with new hosts.

The progress of the individual specimens was not observed after the last week in December, for, unknowingly, *Coccophagus* in the egg and larval stages were introduced into the cages containing presumably parasite-free mealybugs. In view of what eventually happened, it is certain that some *Coccophagus* must have issued and oviposited without being noticed. In January, hundreds of *Coccophagus* emerged unexpectedly. In February, *Coccophagus* began to issue in overwhelming numbers and it became necessary to destroy a surplus each day in order to preserve a balance between the stock of mealybugs and parasites. The surprising rapidity with which *Coccophagus* and the other natural enemies developed made it advisable to rush the entire lot of material to California, where unlimited quantities of host insects were available.

During March, April, and May, 1928, *Coccophagus* were propagated in the insectary of the Citrus Experiment Station at Riverside. The first colonies were liberated in the citrophilus-mealybug-infested areas of southern California during June, and at the same time colonies were offered to the operators of the various local insectaries which were engaged in the mass production of *Cryptolaemus.* On July 24, the first recovery was made, when specimens of *C. gurneyi* were reared from citrophilus mealybugs infesting a sapota tree located in the city of Whittier. After the date when the first recovery was made, specimens were taken in rapidly increasing numbers from all localities where colonies had been liberated and test rearings made. Within a year the species was thoroughly established throughout the greater part of the infested area of southern California and in parts of the San Francisco Bay region. In July, 1929, the propagation of *Coccophagus* was discontinued by the Citrus Experiment Station, as it was considered that the species was thoroughly established.

The Adult.—The female of *Coccophagus gurneyi* can be distinguished by coloration from all other described species of *Coccophagus* with one exception; the body is black, with a conspicuous band of yellow across the base of the abdomen (fig. 2). The body of the male is entirely black and it cannot be so easily recognized as the female (Compere, 1929).

Oviposition.—The adults are slow and deliberate in their movements. When ovipositing, the females are not easily disturbed and they will persist in their efforts unless they are prodded or forcibly removed. Mating and egg laying begin soon after emergence. Adults are long-lived; females have been frequently observed ovipositing more than three weeks after they were confined in cages.

In a series of experiments to obtain egg-laying records, some adults lived for 27 days when confined in a small vial. During their confinement these specimens were given drops of water and sugar and provided with a fresh mealybug each day, which not only served as a host but supplied food in the form of honeydew. In one set of tests, 67 eggs were deposited by a single female within the first 48 hours. This female did not again oviposit until 3 days later, when 17 eggs were laid. Two days later she laid 40 eggs. One female lived for 2 weeks without depositing any eggs. Others produced 1 or 2 eggs daily over a period of 15 days. In the majority of cases, oviposition extended over a period of 15 days when the parasites were confined in small vials. After oviposition ceased the parasites continued to live. One female lived for 27 days and deposited a total of 45 eggs, of which 23 were laid on the first day.

These preliminary data in regard to fecundity are too meager to permit even a rough estimate of the normal reproductive capacity, and they also suggest the probability that experiments with specimens closely confined are not a reliable index of what happens under natural conditions. It is definitely known, from field observations and cage work, that under normal conditions the adults are long-lived and oviposit over a considerable period of time. In the general account, mention was made of a female that issued on November 24, 1927, and was under observation until December 18, when she was mated and then allowed to resume ovipositing.

Fig. 2. *Coccophagus gurneyi* Compere, female.

Citrophilus mealybugs of both sexes and of all stages are attacked by this parasite. In the cages it is not uncommon to see *Coccophagus* ovipositing in the winged males which swarm on the cloth during certain hours of the day. It seems unlikely that *Coccophagus* can develop to maturity in the adult males, but this supposition has not been proved. The immature males, or pupae, contain sufficient food to nourish the *Coccophagus* to maturity. Many of the *Coccophagus* produced in the insectaries for field colonization developed on immature male mealybugs. If the cottony masses which are found in the cages are examined, it is seen that they contain large numbers of male pupae, and parasitized specimens can be detected.

Normally only one egg is deposited in a mealybug. Females do not distinguish between parasitized and unparasitized hosts and, consequently, a single host will often be attacked by more than one parasite. Repeated ovipositions occur in one mealybug when there are too few hosts. This applies to specimens under natural as well as under insectary conditions, as is shown by dissections. Mealybugs

from a locality where the adult parasites are abundant often contain 5 or 6 eggs, the supernumerary ones of which are in the process of being destroyed by the so-called 'phagocytic action.'

Occasionally *Coccophagus* eggs are found in the host's visceral organs or in the ovarian eggs, but generally they are deposited in the body cavity and float out into the solution in which the host is dissected.

When about to oviposit, the female approaches the host in the manner usual to many parasites. A short preliminary examination is made by sensing the mealybug with the ends of the antennae. If satisfied with the preliminary inspection, she stands over the site selected for insertion and flexes the end of the abdomen downward and forward to bring the apex in contact with the host. The tip of the ovipositor is fixed against the derm of the host and then the abdomen is returned to the normal horizontal position leaving the protruded ovipositor extending perpendicularly to the host. Several seconds to three-quarters of a minute, according to the size of the host and the toughness of the derm, elapse while the derm is being pierced. While drilling through the derm the parasite remains motionless, in an upright position, antennae elbowed and hanging downward, the wings in repose. As the tip of the ovipositor penetrates the derm the abdomen is lowered, forcing the exserted ovipositor its full length into the mealybug. Usually the egg is not deposited immediately, but only after the parasite partly retracts and inserts the ovipositor in probing movements. This probing is significant; for if the mealybug is already inhabited the occupant is usually detected by the *Coccophagus*, which then responds differently, according to the type of larva encountered. This is further discussed under the heading, "Biological Interrelations of Host and Parasites."

The Egg.—The egg is of the usual coccophagine shape, elongate, slightly arcuate, and widened anteriorly, as shown in figure 3*A*. The micropyle is usually conspicuous and rather large, being visible in the ovarian eggs as well as in those newly laid. The micropylar end is sometimes folded and flattened like a miniature cap or imperfectly formed pedicel. The chorion is smooth and transparent, clearly revealing the contents which, in the newly laid egg, are opaque, white, and homogeneous. The newly laid egg measures about 0.16 mm long by 0.04 mm wide. The egg enlarges as the embryo develops. Before hatching, the fully formed larva is clearly visible within the transparent chorion. At summer temperature, 27 days elapse from the egg to the adult stage, and the eggs hatch in approximately 4 days.

The Larva.—The newly hatched larvae are not unlike those seen while enclosed in the chorion. At hatching, the alimentary canal contains some material which was obtained while in the egg. After the larva begins to feed, reddish particles appear in the alimentary tract. The first-stage larva has twelve definable body segments, exclusive of the head and tail. The tail is not so attenuated and slender as in some species of *Coccophagus*, and in certain positions it appears much like a thirteenth body segment. The mandibles are small and not easily seen. A drawing of a first instar larva is shown in figure 3*C*.

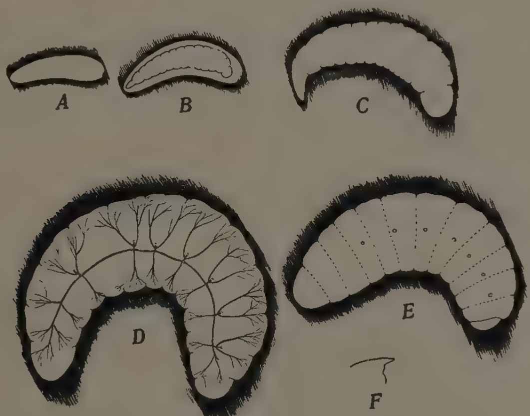

Fig. 3. *Coccophagus gurneyi* Compere. *A*, newly laid egg; *B*, egg just before hatching; *C*, larva several days after hatching; *D*, mature larva showing tracheal system; *E*, larva after voiding meconium; *F*, mandible of mature larva.

No effort was made to count the number of molts and instars. Figure 3*C–E* shows three larval instars.

In only one respect does the larva seem unusual. When fully grown it has only seven pairs of spiracles, while in all the other known species nine pairs of spiracles are usually present. Open spiracles do not appear until the last instar. In the penultimate instar the tracheal system is well developed and seven closed spiracular branches are present.

The fully mature larva completely fills the body of a small or partly grown mealybug, but in a mature mealybug the body is not entirely occupied.

At summer temperatures, on about the seventeenth day after the eggs are laid, the larvae void the contents of the alimentary tract,

pupate, and several days later the pupae begin to blacken. During the summer months about 27 days elapse between egg deposition and the emergence of the adults.

Appearance of Parasitized Mealybugs.—The mummified bodies of mealybugs destroyed by *Coccophagus* are usually grayish or fuscous owing to the dark-colored pupal remains which underlie the hardened parchment-like derm of the host. Specimens occasionally retain the waxy filaments and powder after mummification so that the characteristic dark coloration is obscured. The exit holes through which the parasites issue are usually located dorsally near the posterior end of the host. The pupa lies ventral side downward with its head end at the posterior end of the mealybug. The mummified mealybugs are most abundant in places of concealment, such as under trap bands, in dried leaves, or under loose bark. It seems evident that parasitism causes the mealybugs to desert the exposed feeding areas prematurely in search of a place of concealment.

Destruction of Supernumerary Eggs and Larvae.—As a general rule only one *Coccophagus* matures in a single host. This was thought to be an invariable rule, and it has been so in the case of thousands of specimens examined. Helen Perry, a laboratory assistant who was engaged in making dissections to obtain records concerning the percentage of parasitism in the orchards, first called attention to several specimens of citrophilus mealybugs containing more than one larva. In one particular mealybug, 5 perfectly formed pupae of *Coccophagus gurneyi* were discovered. A possible explanation of this rare situation is that these *Coccophagus* developed as accidental secondaries on *Pseudaphycus angelicus* (How.), a species with gregarious habits that very rarely parasitizes the citrophilus mealybugs in California.

If more than one *Coccophagus* oviposits in a mealybug, or if a single parasite deposits more than one egg in an individual host, none may develop, or only one of these eggs may reach maturity. Supernumerary eggs and larvae are destroyed by some process which appears very similar to the so-called 'phagocytic action' that destroys *Coccophagus* eggs in an immune host such as *Pseudococcus citri* (Risso). Possibly, as believed by some entomologists, the phagocytic action is a secondary process acting upon organisms that have been killed by some more obscure, defensive host reaction. Regardless of the nature of this defensive reaction, it not only kills supernumerary eggs and larvae but it also inhibits the development of the surviving parasite. This is shown by the size of solitary larvae when compared with those that survive in competition. In extreme cases when 10 to 20 or more eggs are deposited by *Coccophagus* in a single mealybug,

all the eggs and larvae as well as the host succumb. In cages where excessive parasitism occurs, it is not uncommon to see hundreds of shrunken, dead citrophilus mealybugs. If dissected, these dead mealybugs will be found to contain numerous dead and dying *Coccophagus* eggs and small larvae. In contrast *P. citri,* a perfectly immune host, will successfully destroy as many as 54 *Coccophagus* eggs without appreciable injury.

Phagocytosis is characterized by the presence of reddish cells which congregate around the eggs or larvae. As the process continues, the cells contract and harden and the entire mass comes to rest in the form of a small black pellet. These pellets usually lodge just beneath the derm of the host, through which they are readily seen.

DESCRIPTION AND BIOLOGY OF TETRACNEMUS PRETIOSUS

The first specimen of *Tetracnemus pretiosus* Timberlake that was reared from mealybugs was obtained from material collected under a piece of loose bark in débris in the citrus orchard of Fred Chilton, at Warrawee, New South Wales, November 19, 1927 (Smith and Compere, 1928). This lone female *Tetracnemus* issued November 27, 1927, and was captured and placed in a vial with some specimens of *Pseudococcus gahani.* She readily oviposited in them. She was next liberated in a jar with a plentiful supply of mealybugs in which to oviposit. On December 7, an inspection of the jar was made and the adult *Tetracnemus* was found dead. At this time she was recognized as being specifically the same as a specimen (the host of which was unknown) that had been collected at random in the Sydney Botanical Garden some time previously.

During January, male *Tetracnemus* began to issue from this jar. On subsequent days a few females were noted. The latter, and no doubt some of the males, were unknowingly introduced into the stock when in the egg or larval stage, concealed within their hosts.

Tetracnemus were reared by thousands on February 19, 1928, when a large quantity of *Pseudococcus gahani* was brought into the laboratory. This material was obtained from the infested mulberry tree that was discovered January 13, 1928, on Bulwara Road, Sydney.

The parasites readily reproduced at the Riverside insectary, and colonies of *Tetracnemus pretiosus* were supplied to the Orange and Los Angeles county insectaries on April 23 and 24, 1928, and at the same time colonies were liberated in the field. The first recovery was

made on August 15, 1928, when *Tetracnemus,* in company with *Diplosis* sp. and *Coccophagus gurneyi,* were reared from *Pseudococcus gahani* infesting a sapota tree located in Whittier. At about the same date, D. W. Tubbs reported rearing *Tetracnemus* from mealybugs collected in Orange County. In every locality where the species was colonized it quickly became established.

The Adult.—The adult female *Tetracnemus* (fig. 4) cannot be briefly described in a way that will permit its ready identification. The original description by Timberlake should be consulted for the

Fig. 4. *Tetracnemus pretiosus* Timberlake, female.

determination of the adults (Timberlake, 1929). The male, which has branched antennae, is more easily recognized than is the female.

The life history of this valuable and interesting species has not been fully worked out.

Oviposition.—The remarkable oviposition habit of this species was demonstrated in Sydney on February 21, 1928, when hundreds of *Tetracnemus* escaped from the material being prepared for shipment to California. Citrophilus mealybugs were hatching at the same time and some of them escaped before the shipping boxes were closed. The *Tetracnemus* were attracted to the newly hatched mealybugs crawling on the boxes and were energetically ovipositing in them, one after another, with hardly a pause between ovipositions.

Female *Tetracnemus* readily, if not preferably, attack very small mealybugs. The long, slender ovipositor is extended from the apex of the abdomen and the parasite faces away from the victim. The ovipositor is plunged into the body of the mealybug on the first thrust and the egg quickly deposited. No particular spot on the host is selected as the site for the insertion of the ovipositor. It may be

thrust into the anterior end of the mealybug just as often as into the posterior end. The evidence indicates that most of the eggs are deposited within the first few days after emergence and that the adults are short-lived.

Temperamentally *Tetracnemus* is very different from *Coccophagus gurneyi;* the former is more active while the latter is slow, deliberate, and apparently more methodical in its habits.

The Egg.—Considerable difficulty was experienced in locating the eggs of *Tetracnemus* after they were deposited in a mealybug. A few eggs were recovered after small mealybugs were exposed to attack and then dissected. Newly deposited eggs are exceedingly small and are not usually detected when the ordinary low powers of a binocular miscroscope are used. They measure about 0.03 mm in length, inclusive of the pedicel, as indicated in figure 5*B*.

The Larva.—The illustrations of the egg and larval stages are not drawn to scale, but the sizes are indicated by actual measurements in millimeters. Presumably five, or possibly six, larval instars were observed. The notes and drawings illustrating the life history of *Tetracnemus* were obtained by a study of specimens dissected from mealybugs at intervals during the development of a single generation of parasites. This life history study should be verified and amplified, for there is uncertainty regarding several very interesting stages.

Pseudococcus gahani in a cage were exposed to the attack of *Tetracnemus* on August 9, 1928, and then isolated. By August 21, the more advanced larvae had consumed the entire body contents of the mealybugs and were casting their meconia. The mature larva orients itself parallel to the long axis of the host and expels the meconium in one end, where it appears as a 'black cap.' The mealybugs remain alive and active until the parasitic larvae are almost fully grown. A single specimen possibly representing an instar not illustrated, was discovered. The specimen had cast its meconium and the mandibles were distinctly serrated at the apex with three minute, acute teeth. The generation of parasites that started August 9, began to issue September 1, 1928, a period of 23 days elapsing from the deposition of the egg to the emergence of the adults.

The incubation period was not determined. On the fourth day the specimens had increased to about eight times their original size and had assumed the shape and appearance of larvae, although still enclosed in the transparent chorion. Presumably these 4-day-old specimens were embryos within the eggs and the chorion had enlarged and closely adhered to the developing larvae. Figure 5*C* and *D*

represents this stage. The 5-day-old specimen shown in figure 5*E* does not show an increase in size compared to those noted the previous day, and it is still enveloped by the closely adhering, form-fitting chorion, but the embryo or larva shows considerable development.[5] Specimens dissected from mealybugs on the seventh day were free

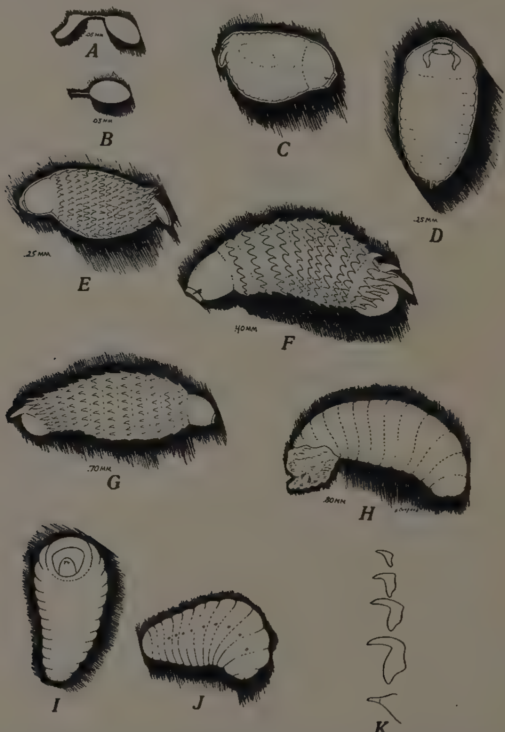

Fig. 5. *Tetracnemus pretiosus* Timberlake. *A*, ovarian egg; *B*, newly laid egg; *C–D*, larva just before hatching, lateral and ventral views; *E–J*, larval instars; *K*, series of larval mandibles. (The series of mandibles are drawn to scale, the other figures are not.)

of the enveloping chorion and had grown to one and one-half times the size of the larvae that were observed on the fifth day. The 7-day-old specimens showed the tracheal trunks beginning to develop in the

[5] It should be noted here that the eggs laid by this adult *Tetracnemus* were deposited during a period of 12 hours, so that a discrepancy may appear when the larvae are identified by their age as counted in days.

region of the third segment; the tubercle-like projections and the head were relatively smaller in proportion to the size of the body; while a bulging posterior protrusion had developed. Larvae 8 days old, counting from the deposition of the egg, had increased to almost twice the size of the specimens noted on the seventh day; the tracheal system was similar but the head and projections were relatively smaller.

A 9-day-old larva is shown in figure 5*H*. The last molt skin is adhering to the posterior end, the tubercles characteristic of the preceding instars have disappeared, the head has undergone a marked change, and the mandibles and mouth parts are radically altered and reduced. Larvae removed from mealybugs on the twelfth day were about ready to pupate and did not possess any distinctive characteristics which would readily distinguish them from the larvae of many other encyrtid parasites. In this stage nine pairs of open spiracles appear and the segmentation is distinct. The fifth and largest pair of mandibles, as shown in figure 5*K*, is associated with this instar. It is possible that the largest mandibles figured possess minute apical teeth, but if so, they were concealed by their position.

The series of mandibles is drawn to scale, and they are associated with the specimens representing the different instars as figured.

So far as observed, only one larva develops in a single mealybug. The process by which supernumerary eggs and larvae are destroyed was not noted.

Appearance of Parasitized Mealybugs.—It is not always easy to distinguish between mealybugs destroyed by *Tetracnemus* and those destroyed by *Coccophagus*. Generally, however, the host remains of *Tetracnemus* are characterized by the paler color of the 'mummy,' and by the more uniform and regular appearance of the meconial discharge which appears at one end, giving the 'black cap' appearance.

The Present Status of Tetracnemus in California.—In the areas where *Tetracnemus* was established before *Coccophagus*, it rapidly became very abundant and indicated that it was able to bring an infestation under control. With few exceptions the range of *Tetracnemus* was soon overlapped by that of *Coccophagus* and the latter species became dominant. Occasionally limited areas were found where *Tetracnemus* was not replaced and effectively controlled the mealybugs. *Tetracnemus* is now generally present throughout the infested area but in smaller numbers than is *Coccophagus*. There is evidence indicating that during the past two seasons (1930 and 1931) the *Tetracnemus* population gained relative to that of *Coccophagus* during the summer months, and lost during the winter months.

HABITS OF ANUSOIDEA COMPEREI

Anusoidea comperei Timberlake is presumably a primary parasite of the citrophilus mealybug, *Pseudococcus gahani* Green. For a discussion of the adult characters of this species the reader is referred to the original description (Timberlake, 1929).

On December 4, 1927, in Sydney, a single female specimen of *Anusoidea* issued from an undetermined mealybug. This mealybug was segregated in a small vial; for it was obviously parasitized at the time of collection. Soon after the parasite issued she was tested in a vial with samples of *Pseudococcus gahani.* She readily oviposited in them. After being allowed to oviposit for a short period, this female was isolated. Since she was a virgin it was anticipated that her progeny would be males. This proved to be the case, for male specimens appeared January 2 to 7, 1928. During the interval of waiting for the appearance of male specimens, the female was regularly fed and kept in a cool place. She was alive in January when her male offspring issued and she was then mated to them. After being fertilized she was allowed to resume oviposition. Both male and female progeny resulted from this union, and began to issue February 10. When mating couples were noticed they were captured and placed in other cages. Unfortunately, practically the entire third generation of *Anusoidea* was consigned to cages which eventually developed a large number of *Coccophagus.* Only a few male specimens of a fourth generation matured. The loss of *Anusoidea* was possibly due to replacement while in the larval stage by *Coccophagus.* It was not introduced into California.

HABITS OF MIDAS PYGMAEUS

It is not known whether *Midas pygmaeus* Blackburn (fig. 6) is permanently established in California. During 1929, prior to the general control of the mealybug by parasites, occasional specimens of *M. pygmaeus* were taken from under the burlap bands in areas where the colonizations were made. *Midas* was imported into California at the same time as were the internal parasites of *Pseudococcus gahani.* It was introduced with the expectation that it would be of considerable value, for in New South Wales it occurred generally wherever *P. gahani* was found.

The larvae of *Midas pygmaeus* (fig. 7) were first collected in the Sydney Botanical Garden, where specimens were discovered in cracks and places of concealment, feeding on the eggs of the few citrophilus mealybugs that reached maturity. *Midas* was never taken working on either *Pseudococcus citri* or on *P. maritimus*, although several severe infestations occurred in proximity to the places where *Midas* was collected. Very often the presence of a few citrophilus mealybugs on *Grevillea, Pittosporum,* or *Nerium* was indicated by the presence of a stray *Midas* larva.

Fig. 6. *Midas pygmaeus* Blackburn, adult.

Fig. 7. *Midas pygmaeus* Blackburn, larva.

One peculiar trait of *Midas* is its habit of shunning the light and remaining concealed. It is not easy to collect adults propagated in cages because they remain in the cracks of the soil or work down around the potato tubers.

An interesting reference to *Midas pygmaeus* was made by Albert Koebele in 1893, when he wrote:

> This insect was bred from a white, tufty larva found upon orange at Paramatta, New South Wales. It was also collected in considerable numbers at Toowoomba, Queensland, upon the same tree. Became quite abundant at Sydney during March upon oleander and *Pittosporum* infested with a species of *Dactylopius* upon which they appear to feed. Was also found at Mulgoa, New South Wales, upon eucalyptus. Many specimens sent to California.

In the unpublished letters of George Compere there are records showing that he made shipments of *Midas* to California from New South Wales.

A stock of *Midas pygmaeus* is still maintained in some of the local insectaries and occasional colonizations are being made.

DESCRIPTION AND BIOLOGY OF DIPLOSIS SP.

This species of *Diplosis* has not been determined. It is possibly the same as the species discovered by Albert Koebele in Sydney and reported by him in 1893 under the name *D. koebelei* Skuse MS.

Diplosis sp. was reared from various mealybugs collected in the Botanical Garden and in the vicinity of Sydney during the period from November to February, 1927. The species readily propagated on *Pseudococcus gahani* when placed in the cages, and multiplied so rapidly that it was necessary to destroy the excess of adults continually in order to preserve the stocks of mealybugs.

Diplosis was imported into California in March, 1928, with the other natural enemies of *Pseudococcus gahani* from Sydney. Colonies were placed in the orchards during the spring of 1928 and the first recovery of adults was made August 15, 1928. As in the case of the other natural enemies of citrophilus mealybugs, the Orange County and Los Angeles County insectaries took the lead in the mass production and distribution. *Diplosis* rapidly established itself where it was colonized. Occasional *Diplosis* larvae were found on mealybugs submitted for examination during the 1928–29 season. Fewer recoveries were made during the 1929–30 season. This species is thought to be permanently established in California, but its influence is negligible.

The life history of *Diplosis* was worked out by Mumtaz Arif, a graduate student located at the Citrus Experiment Station during the summer of 1929. His studies have not been published.

The following data were obtained while engaged in the work of propagating the species; no special effort was made to obtain life-history notes.

The Adult.—The adults are not easily handled in confinement. When placed in small containers they injure themselves in their continued efforts to escape. In cages or large containers their behavior is more nearly normal. In the small containers individual specimens lived not more than 4 days. The adult life under cage conditions was not ascertained. The peculiar habit of congregating on spider webs, which is commonly seen with many cecidomyids, is highly developed in this species. In the cages it is a common sight to see dozens of specimens swinging to and fro in unison on a single web.

The Larva.—If taken associated with *Pseudococcus gahani*, the larvae of *Diplosis* can be readily recognized since the only other maggots likely to be found associated with this insect are those of *Leucopis*. *Leucopis* has grayish larvae, while those of *Diplosis* are orange with the digestive tract appearing as a dark longitudinal streak. The larval period averages about 7 days during the summer months. Larvae readily feed upon all stages of mealybugs. They pierce the host and suck out the fluid contents.

The Pupa.—Pupation usually takes place about 9 days after the eggs are laid. Pupae are usually found in old egg masses or in proximity to the infestations. The pupal stage lasts about 4 days on the average.

CHRYSOPA RAMBURI AS AN ENEMY OF PSEUDOCOCCUS GAHANI

The larvae of *Chrysopa ramburi* Cameron were especially conspicuous on various coccid-infested shrubs in the Sydney Botanical Garden. The larvae are trash carriers and are very active, running along the limbs and twigs with their backs matted with the remains of coccids and other débris. This lacewing reproduced readily in the cages on *Pseudococcus gahani*. A colony was brought to California and living specimens were supplied to several insectaries. It is doubtful if this species is established in California.

BIOLOGICAL INTERRELATIONS OF HOST AND PARASITES

Timberlake (1913) first recorded the fact that under certain conditions *Coccophagus lecanii* (Fitch) is able to develop on other scale parasites. Although he stated very plainly that this type of parasitism was accidental and that true primary parasitism was the rule, the statement that this valuable species occasionally developed hyperparasitically was quoted by certain authors without being qualified, and the species was, therefore, recorded as a hyperparasite. The genus *Coccophagus* includes some of the most valuable scale-destroying parasites. It is possible that most of the species which have solitary larvae are capable of development on other primary parasites, or upon individuals of their own species under certain conditions. This is the case with *C. gurneyi*. The existence of such a habit is of no economic significance, since there is no selection by the

parasite of parasitized hosts in preference to unparasitized ones. It is, however, of considerable interest biologically.

If an ovipositing *Coccophagus* attacks a mealybug which is already inhabited by a larva, the egg originally intended for the mealybug will be deposited either within or upon the first occupant. Timberlake recorded the remarkable fact that when *C. lecanii* develops hyperparasitically its habits undergo a radical change and it develops as an ectoparasite on the first inhabitant, when both are within the scale. It has been found that *C. gurneyi* is capable of both ecto and endoparasitic development in relation to the first inhabitant. The first evidence of this ability to develop either way was observed when both *C. gurneyi* and *Tetracnemus pretiosus* were being propagated in the same cages. When these mixed populations occurred, *Coccophagus* was always dominant and in time completely eliminated *Tetracnemus.*

Tetracnemus deposits the major part of its eggs during the first few days and then dies. In contrast, *Coccophagus* oviposits over a period of about three weeks. Consequently, after the first week some of the ovipositing *Coccophagus* chance upon some of the mealybugs inhabited by *Tetracnemus* larvae. When an ovipositing *Coccophagus* encounters a *Tetracnemus* larva, it deposits the egg originally intended for the mealybug within the body of the *Tetracnemus.* Many of the mealybugs which were exposed to excessive numbers of *Coccophagus* and *Tetracnemus* in the same cage were found to contain *Tetracnemus* larvae having from one to six or more *Coccophagus* eggs inside them. Frequently the *Tetracnemus* larvae were distended by being completely filled with *Coccophagus* eggs. In many cases in addition to the eggs found in the *Tetracnemus* larvae, parasite eggs were found free in the mealybug's body. Although *Coccophagus* does not discriminate between parasitized and unparasitized mealybugs, it seems evident that oviposition occurs in the primary larva in preference to the mealybug itself whenever a previously parasitized host is attacked. Almost invariably when a primary occupant is met by the probing ovipositor of a *Coccophagus,* the egg is placed either upon or within it. However, if the first occupant is not detected by *Coccophagus,* then the egg is deposited in the body of the mealybug itself.

When this habit of *Coccophagus* was discovered, it was thought that possibly it could develop on a parasite within a mealybug which was immune to parasitism by *Coccophagus.* For this experiment *Leptomastidea abnormis* (Girault) inhabiting *Pseudococcus citri* were

used.[6] A remarkable thing occurred. If the *Leptomastidea* larvae were small and were not detected by the ovipositing *Coccophagus*, the eggs were deposited free in the mealybug's body where they were destroyed by the physiological processes which render this species of mealybug immune to parasitism by *Coccophagus*. However, if the ovipositing *Coccophagus* chanced upon the larva of a *Leptomastidea*, it deposited its eggs upon the body of this primary inhabitant and became ectoparasitic in relation to it. On dissection the *Coccophagus* eggs were found adhering to the derm of the *Leptomastidea* larvae. The ultimate fate of *Coccophagus* growing on *Leptomastidea* is determined by the condition of the mealybug. If the mealybug has not been seriously weakened by the *Leptomastidea*, the normal defensive reaction of the mealybug destroys the *Coccophagus* eggs while they are in place on the body of the *Leptomastidea;* but, if the *Leptomastidea* has consumed the fluids of the mealybug, the protective reaction of the mealybug is destroyed, and the *Leptomastidea* has rendered itself vulnerable to *Coccophagus*.

Under certain conditions *Coccophagus gurneyi* is capable of destroying mature *Leptomastidea abnormis* larvae and prepupae, but it appears to be incapable of developing to maturity on these hosts. Out of hundreds of trials, not a single *Coccophagus* successfully completed its development on *Leptomastidea*. Under suitable conditions the *Coccophagus* eggs will hatch and the larvae will destroy *Leptomastidea*, but according to our observations *Coccophagus* always fails to reach maturity, and all three insects die. The influence of *Coccophagus* on *Leptomastidea* is believed to be negligible.

Coccophagus reacts to finding its own larva in a mealybug much the same as it does when accidentally encountering a *Tetracnemus* larva, that is, it deposits its egg within the first inhabitant, which is eventually consumed by the larva that hatches last.

When developing on other parasitic larvae, *Coccophagus* larvae grow much faster than they do when developing on the mealybugs themselves. This has been observed in the case of other species which have this habit. It is suggested that the more rapid development is a result of the use of food which has been already elaborated by a prior inhabitant of the host.

Although *Coccophagus* eggs and larvae normally develop in the body fluids of mealybugs, they are capable of development when isolated in dry containers if placed on a larva of *Leptomastidea*.

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[6] *Leptomastidea* is a primary parasite of *Pseudococcus citri* (Risso), a mealybug immune to parasitism by *Coccophagus*, although the latter readily oviposits in it.

An occasional young larva of *Tetracnemus pretiosus* was found occupying a mealybug in company with a *Coccophagus* larva, but the ultimate outcome of this association was not determined. When small *Tetracnemus* and *Coccophagus* larvae are found developing within the same host it is probable that oviposition of both species was almost simultaneous. In the great majority of cases where competition was observed *Coccophagus* had oviposited after *Tetracnemus* had reached the larval stage and *Tetracnemus* then became the host of *Coccophagus*.

NUMERICAL RELATIONS OF HOST AND PARASITES

Multiple Parasitism.—It has been maintained by some entomologists (Pemberton and Willard, 1918) that it is a mistake to introduce for control purposes two or more species of entomophagous insects attacking the same stage of the host, for, according to this theory, the resulting competition reduces the total controlling effect to a point below that which would have occurred if only the more prolific species had been introduced. Regardless of the soundness of this theory, it is largely a matter of academic interest rather than of practical concern, because of the extreme difficulty, if not impossibility, of predicting how an insect will respond to a new environment, and particularly to the biotic phases of that environment.

It is well known that the potential reproductive capacity of a parasite bears no direct relation to the ability of that parasite to maintain its host at a low population density. If such a direct relation existed, the polyembryonic species would ordinarily be the most effective, when, as a matter of fact, they are probably of very little economic importance as compared to many of the monembryonic species. Reproductive potential, therefore, cannot be used as a criterion by which to make a selection of entomophagous insects for introduction into a new habitat. Neither can it be safely concluded that of two parasites attacking the same host in its native home, the one which destroys the greater percentage of hosts is the more valuable one to introduce. This assumption often proves incorrect, as it does in the present case; *Tetracnemus* was much more effective in Australia, while in California *Coccophagus* seems to be much more effective.

If the theory of the injuriousness of multiple introductions is accepted, it would be necessary to obtain a complete knowledge of the ecology of *all* the insect enemies of a particular host throughout

the world and also of the insect enemies of related hosts, before any species could be introduced. The absence of any reliable criterion by which to judge the comparative value of entomophagous insects for the purpose of biological control, makes it apparent that this theory must be largely disregarded in practical work. It is essential that the introduction of obligatory secondary parasites be avoided, but beyond this there is as yet no known criterion upon which to base further efforts at selection.

Certain theoretical objections to the hypothesis that multiple introductions are injurious have been advanced in another paper (Smith, 1929). The introduction of *Coccophagus* and *Tetracnemus* into California has provided some interesting data on the practical aspects of this question.

As has been previously mentioned, when colonies of both *Tetracnemus* and *Coccophagus* are introduced into a cage heavily stocked with citrophilus mealybugs, *Coccophagus* rapidly becomes dominant and in time completely eliminates *Tetracnemus*. Under such conditions there occurs a very high percentage of parasitism and consequently a large amount of overlapping. It is to be expected that *Tetracnemus* will disappear, since *Coccophagus* is the victor when the two meet in competition and since there are enough adult *Coccophagus* produced to parasitize *all* the mealybugs in the cage. In the field, however, the condition is very different.

If the parasites are of any great value, they will maintain the mealybug population at a low density. As the density of the host becomes reduced the percentage of parasitism must for obvious reasons become reduced also. This reduction in parasitism is naturally accompanied by a reduction in overlapping of the two species of parasites, so that the ratio

$$\frac{\text{number of hosts parasitized by } \textit{Tetracnemus}}{\text{number of hosts parasitized by } \textit{Coccophagus}}$$

varies inversely with the density of the host population. A low density of the host *must be maintained* by the parasites if they are to be of much practical value. When the density of the host is low there is a minimum of overlapping and, therefore, slight effect by one parasite on the other. Consequently, it seems entirely reasonable to conclude that these two parasites are more effective than either one alone would have been. Under such conditions each species destroys host individuals which would have escaped destruction by the other, if the parasites have slightly different habits and habitats.

In this case another advantage of two species over one is their different response to the same temperatures. *Tetracnemus* is very scarce during the winter months, while *Coccophagus* is active throughout the cold weather and develops two generations to one of its host. This winter activity of *Coccophagus,* at a time when the mealybug population is normally low, is most effective since it materially reduces the overwintering mealybugs that produce the spring brood, which caused the greatest damage in the past. During the summer, however, *Tetracnemus* causes a considerable mortality of mealybugs.

The presence of heavy ant infestations also produces a different effect on the two species. *Coccophagus* is very slow and deliberate in oviposition, whereas *Tetracnemus* oviposits very quickly. For this reason ants have more opportunity to interfere with the activities of *Coccophagus* than of *Tetracnemus.* In the infestations where the mealybugs were protected by ants, dissections have shown that *Tetracnemus* was more abundant, relative to *Coccophagus,* than was the case in the average sample from ant-free locations.

Influence of Parasites on Population Density of Mealybugs.—During the past three years many thousands of mealybugs, representing hundreds of samples from distinctly varying climatic zones in California, have been dissected for the purpose of obtaining the percentage of parasitism. This work was undertaken as a part of the process of establishing the parasites in all the infested areas, and also to obtain a better idea of their progress. It was realized that the percentage of parasitism, when not correlated with figures representing the population density of the host, is of little or no value in determining to what extent the parasites influenced host population density. It was not possible, however, with the means at our disposal, to obtain figures on population density of sufficient reliability to make them useful for this purpose.

The percentage of parasitism, as exhibited by the samples, ranged from 20 to 60 per cent, with occasional samples running much higher, and a few 100 per cent parasitized. In considering this question, however, it is necessary to bear in mind that the actual destruction of mealybugs by parasites was considerably higher than the samples indicated. Many of the mealybugs were small and would have been liable to attack for several weeks if they had not been collected. Often the specimens were collected in protected places, as between two fruits, where they were inaccessible to parasite attack. This was particularly true in places where the mealybugs had become extremely scarce. Some came from ant-infested trees.

It has frequently been observed that the presence of a parasite larva within a mealybug results in abnormal activity of the host insect. The principal effect of this kind is that it intensifies or advances the reproductive instincts of the females, causing them to migrate down the trunk of the tree when they are about half grown, when ordinarily they wait until they are full grown and ready to deposit their eggs. Bands placed about trees become packed with parasitized half-grown mealybugs, when in the absence of parasites it would have been at least two weeks before this migration took place. A result of this abnormal migration induced by parasitism is that large numbers of parasitized mealybugs leave the trees. Therefore, the samples collected for dissection have a disproportionate number of unparasitized hosts.

It is also necessary to bear in mind that there are approximately two generations of parasites to one of mealybugs, particularly in the cooler seasons. If a sample of mealybugs is dissected and only 50 per cent is found to be parasitized, this does not mean that only 50 per cent of the generation which they represent is destroyed by parasites. Before the surviving mealybugs mature, a second generation of parasites occurs and if these also destroy 50 per cent of the same generation of mealybugs, there is a total destruction of 75 per cent, although only 50 per cent of the mealybugs would contain parasites at any one dissection. It is obvious, therefore, that the actual percentage of destruction of mealybugs by parasites must in most cases be far higher than the dissections have indicated.

The percentage of parasitism, however, taken by itself, is of relatively little value in judging the effect of a parasite on the population density of its host. The general tendency to overestimate the value of such figures for this purpose must be guarded against. Insect enemies are only one of many causes of mortality of a plant-feeding insect, and many of these factors are interdependent in their action. Therefore, it is extremely difficult to determine how the presence or absence of any one factor, such as parasites, will influence the population of the organism against which it operates. A high percentage of destruction by one factor can be important or unimportant, according to whether it replaces or does not replace some other cause of mortality.

It is important to recognize that the percentage of parasitism means little, from a control standpoint, unless correlated with host population density. It is obvious that 50 per cent destruction when there are 100 mealybugs per tree gives a more satisfactory control than 90 per cent when there are 1,000 mealybugs per tree; yet esti-

mates of the importance of parasites are almost invariably given in percentage of hosts attacked with no reference to the host population density.

There is a decided tendency for the percentage of parasitism to increase as host density increases, and to decrease as host density decreases. For this reason a parasite which is capable of destroying 99 per cent of its host where the latter is abundant, may, by its own effectiveness, so reduce the host population that the percentage of parasitism drops to a relatively low figure. It is a mistake, therefore, to assume, because a parasite is destroying only a small percentage of its host when the host is scarce, that the parasite has no important effect on the maintenance of a low host population density. It may be *the important* factor.

When the parasites of the citrophilus mealybug were first introduced the host population density was high, and very few mealybugs in the heavily infested groves escaped attack. As the mealybug population declined, there has been a corresponding decline in the percentage of parasitism, as shown by the average sample.

ECONOMIC EFFECT OF INTRODUCED PARASITES

Since the discovery of *Pseudococcus gahani* Green in California in 1913, this mealybug has gradually and with considerable rapidity spread until it is now generally distributed in most of the regions in which it is capable of developing. In southern California it became a major pest of citrus trees and fruit, while in the northern part of the state it was the most troublesome pest of ornamentals and in some localities did considerable damage to deciduous fruits, particularly pears and apples.

In spite of the efficient work of the local insectaries in the mass production and distribution of *Cryptolaemus montrousieri,* the number of groves in which the control was unsatisfactory increased each year. As stated in the introduction, in 1927 the condition became so serious as to make it necessary to find a means of improving the situation. This led to the exploration in Australia and to the discovery and successful introduction into California of the insect enemies of the citrophilus mealybug discussed in this paper.

During the summer of 1928, after the establishment of the parasites, there was a rapid increase and dissemination of both *Coccophagus* and *Tetracnemus,* and in the spring of 1929 there was a very appreciable reduction in the number of mealybugs in the districts

where the parasites had been thoroughly established. During 1929 there was carried out, largely by certain local insectaries, an extensive production and distribution of *Coccophagus* and to some extent of *Tetracnemus,* so that by the spring of 1930 practically the entire infested citrus acreage in southern California had been colonized and the parasites thoroughly established. In the spring of 1930, at the time of the year when the so-called 'peak hatch' of mealybugs had usually taken place, this phenomenon failed to occur, the parasites having so reduced the overwintering mealybugs that the spring hatch was insignificant from an economic point of view. Throughout the following year, 1931, this favorable condition has been maintained; no infestations of any economic importance have occurred in any of the areas where the parasites have been thoroughly established, and this now includes all of the infested citrus districts of southern California. In northern California, around San Francisco Bay, where this mealybug had been a nuisance in gardens and parks, the establishment in 1929 of these parasites has resulted in control of the pest. It is now found only on occasional plants which are heavily infested with Argentine ants. In the Monterey Bay region, however, where the parasites have only recently been released and in very small numbers, the citrophilus mealybug infestation has been so heavy as to kill a considerable amount of wild growth in the hills, and has been so abundant on shade trees in at least one city that the fire department has been engaged in washing the honeydew from the sidewalks and streets.

There is no method known at the present time for measuring accurately the quantitative effect of separate environmental factors on the population density of a phytophagous insect. Conclusions must still be based on general field observation, and the contention that the disappearance of injurious infestations of the citrophilus mealybug is due to the work of *Coccophagus* and *Tetracnemus* is based on the observation that without exception the absence or occurrence of serious infestations of the pest has been positively correlated with the presence or absence of the parasites. During the past three years there has been a sufficient number of heavy infestations in localities where the parasites were not present to give reliability to the conclusions. These infestations served as check plots and demonstrated that the generally low population level of the mealybug was a result of the work of the parasites and not due to climatic influences unfavorable to the mealybugs. Invariably when the parasites later became well established in these localities, the mealybug population level took a decided, and apparently permanent, drop.

LITERATURE CITED

COMPERE, H.

1928. Successful importation of five new natural enemies of the citrophilus mealybug. California Citrograph **13**:318, 346–349.

1929. Description of a new species of *Coccophagus* recently introduced into California. Univ. California Pubs. Ent. **5**:1–3, *2 figs.*

1931. Revision of the species of *Coccophagus*. U. S. Nat. Mus. Proc. **78**: 1–132.

FERRIS, G. F.

1927. Mealybugs. California State Dept. Agr. Mo. Bul. **16**:336–342.

PEMBERTON, C. E., and H. F. WILLARD.

1918. Interrelations of fruit-fly parasites in Hawaii. Jour. Agr. Research **12**:285–295.

SMITH, HARRY S.

1929. Multiple parasitism: its relation to the biological control of insect pests. Bul. Ent. Res. **20**:141–149.

SMITH, HARRY S., and H. M. ARMITAGE.

1931. The biological control of mealybugs attacking citrus. California Agr. Exp. Sta. Bul. **509**:1–74, *21 figs.*

SMITH, HARRY S., and H. COMPERE.

1928. Establishment in California of newly introduced mealybug parasites from Australia. California Citrograph **14**:5.

TIMBERLAKE, P. H.

1913. Preliminary report on the parasites of *Coccus hesperidum* in California. Jour. Econ. Ent. **6**:293–303.

1929. Three new species of the hymenopterous family Encyrtidae from New South Wales. Univ. Calif. Pubs. Ent. **5**:5–18, *2 figs.*